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South American anoles: *Anolis apollinaris* Boulenger 1919,
a relative of *A. biporcatus* Wiegmann (Sauria, Iguanidae)

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ABSTRACT. *Anolis apollinaris* is a central Andean derivative of *A. biporcatus*, probably from an earlier invasion of South America than that which has provided the present Colombian, Ecuadorian, and western Venezuelan populations of the latter species.

Anolis apollinaris Boulenger 1919 was described from a unique type, a female, said to come from "near Bogota." The description made no mention of relationships.

The next mention of the species was made by Burt and Burt (1931: 255), who referred numerous Colombian specimens in the American Museum to this species. They suggested that the species belonged to the "chrysolepis stock" but also said that their specimens closely resembled *A. gemmosus* of Ecuador with which they believed *A. apollinaris* "may prove to be identical or subspecifically allied." An examination of the type of *apollinaris* in the British Museum shows that these statements of relationships are entirely mistaken and that the specimens referred to the species by Burt and Burt—one specimen received in exchange from the American Museum by the Museum of Comparative Zoology—are misidentified.¹

¹ The type of *A. gemmosus* O'Shaughnessy has also been examined. It is not of *chrysolepis* stock nor related at all closely to the two species misidentified by Burt and Burt as *A. apollinaris*. The affinities of *A. gemmosus* are with *A. fasciatus* Boulenger and *A. andianus* Boulenger.

A correct judgment on the affinities of *A. apollinaris* was made by E. R. Dunn in 1944 (p. 25), who at that time reported:

"The Instituto de La Salle has a specimen of this lizard (described from 'near Bogota') from Paime, Cundinamarca, 1038 meters. A number of students have overlooked the statement that this is a large *Anolis* (type head-body length 106 mm) and misapplied the name. Thus the "*Anolis apollinaris*" of Burt and Burt (1921 [sic], p. 255) is not Boulenger's species but a composite of two smaller species, *incompertus* Barbour from Villavicencio and *mariarum* Barbour from Medellin¹. True *apollinaris* is allied to *solifer* of Santa Marta and *copei* of Central America."

The two latter names are now regarded as synonyms of *biporcatus* (see Williams, 1966) and it is with this species, which ranges from Mexico to Ecuador, that *apollinaris* requires comparison.

Brother Niceforo Maria of the Instituto La Salle tells me that Dunn's specimen of *A. apollinaris* was one of many specimens destroyed in a fire at the Institute in 1948. Fortunately, a number of previously unreported specimens have been discovered, one in the Institut Royale (Brussels), a series in the Zoologische Staatsammlung (Munich) and three, indeed, in more recent collections of the Instituto La Salle (ILS), and two more in the American Museum of Natural History (AMNH).

On the basis of these new specimens and the type specimen at the British Museum (BM), I present a revised standard description of the species:

Anolis apollinaris Boulenger

Type. BMNH 1919.3.6.7 (1946.8-13.22), from near Bogotá, Cundinamarca, Colombia.

Referred specimens. (All Colombia.) *Antioquia* (all Cauca Valley): AMNH 38725, Sabanalarga; ILS 81, Puerto Antioquia. *Caldas*: ILS 101, Pueblo Rico. *Cundinamarca*: Brussels 3580, La Esperanza, 1250 m; ILS 65, Paime; ILS 106, Quipile; Munich 427-432, San Pablo, west side of cordillera between Bogotá and La Dorada. "Western Colombia": AMNH 4844.

¹ *A. incompertus* Barbour is a composite species: specimens from Villavicencio are *A. chrysolepis scyphus* Cope and, from near Bogota, *A. tropidogaster* Hallowell. *A. mariarum* Barbour is a synonym of *A. antonii* Boulenger. All types have been examined.

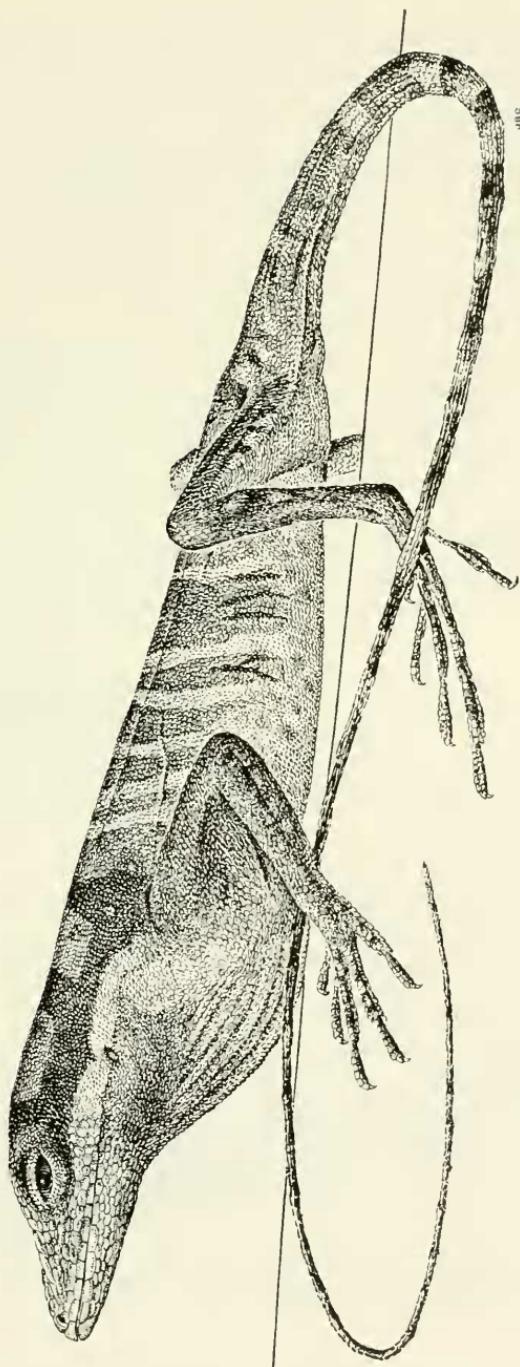


Figure 1. *Anolis apollinaris* Munich male, No. 423. Lateral view.

Diagnosis. Allied to *biporcatus* Wiegmann and its subspecies *parvauritus* Williams but differing in color, in one or no scales separating nasal from rostral, and in a modally higher number of lamellae under phalanges ii and iii of the fourth toe.

Head. Head scales small, sharply uni- or tricarinate. Ten to thirteen scales across snout between second canthals. A distinct frontal depression, scales within it not smaller than surrounding scales. Five to nine scales border rostral posteriorly. Circumnasal scale separated from rostral by one small scale or in contact. Six to seven scales between circumnasals dorsally.

Supraorbital semicircles separated from each other by 2-4 scales, from the supraocular disk by one row of smaller scales. Supraocular disk not very distinct, of 4-12 keeled scales grading laterally into granules. One to three overlapping elongate supraciliary scales, continued posteriorly by granules. Anterior corner of supraocular filled by larger subgranular scales. Canthus sharp, of 6-7 overlapping scales, the first and second or second and third the largest. Five to seven loreal rows, subequal or the uppermost largest. Temporal scales granular. A distinct double line of enlarged intertemporal scales. Supratemporals granular, slightly smaller than

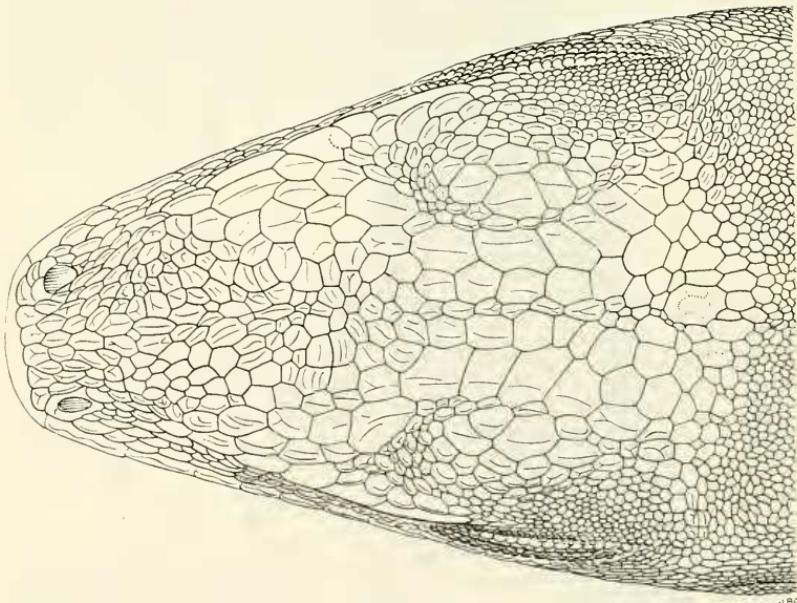


Figure 2. *Anolis apollinaris* Munich No. 422. Dorsal view of head.

temporals. Scales surrounding interparietal moderately to abruptly enlarged, swollen, largest anteriorly and laterally. Interparietal less than or greater than ear, separated from semicircles by 3-4 scales on each side.

Suboculars separated from supralabials by one row of scales (or narrowly in contact), anteriorly separated from canthal ridge by one scale, posteriorly continued by an indistinct double row of smaller scales. Seven to eight supralabials to center of eye.

Mental slightly wider than long, in contact with 4-8 scales between supralabials posteriorly. Sublabials not well differentiated. Central throat scales quadrangular, swollen, gradually increasing in size laterally.

Dewlap. Dewlap in male large with close-packed scales. A gular fold only in female, moderate, scales rather closely packed.

Trunk. Middorsals slightly enlarged, swollen, keeled. Dorsal and flank scales keeled, subequal. Ventrals larger, weakly keeled, imbricate, *not mucronate*.

Limbs. Largest fore and hind limb scales strongly unicarinate, except at knee and elbow, smaller than largest ventrals. Supradigital scales multicarinate. Twenty-four to twenty-seven lamellae under phalanges ii and iii of fourth toe.

Tail. Slightly compressed, almost evenly scaled all round. Verticils indistinct. All scales keeled. Enlarged postanals in male.

Size. Type: 106 mm snout-vent length.

Comparison. Table 1 lists the major features differentiating *A. apollinaris* and *A. biporcatus*. I comment on each of these features below:

1. *Scales in narial area.* The exact pattern of the scales surrounding the naris and their relation to the rostral have been repeatedly used in lizards generally (e.g., geckos), and this pattern has also proved empirically very useful at the species level in *Anolis*. Published examples of the utility of this character at the species level are Ruibal and Williams (1961) and Lazell (1964). Although, like all squamation characters in *Anolis*, these patterns are subject to some intraspecies variation, they are rather surprisingly constant. Frequently a single pattern is consistently maintained; this is usually a simple one. More complex patterns tend to greater variation but the variations are readily derivable from the modal condition (Fig. 3). The pattern of *apollinaris* is always simpler than that of *biporcatus* and may be more primitive. (The judgment that this pattern may be more primitive is based not upon

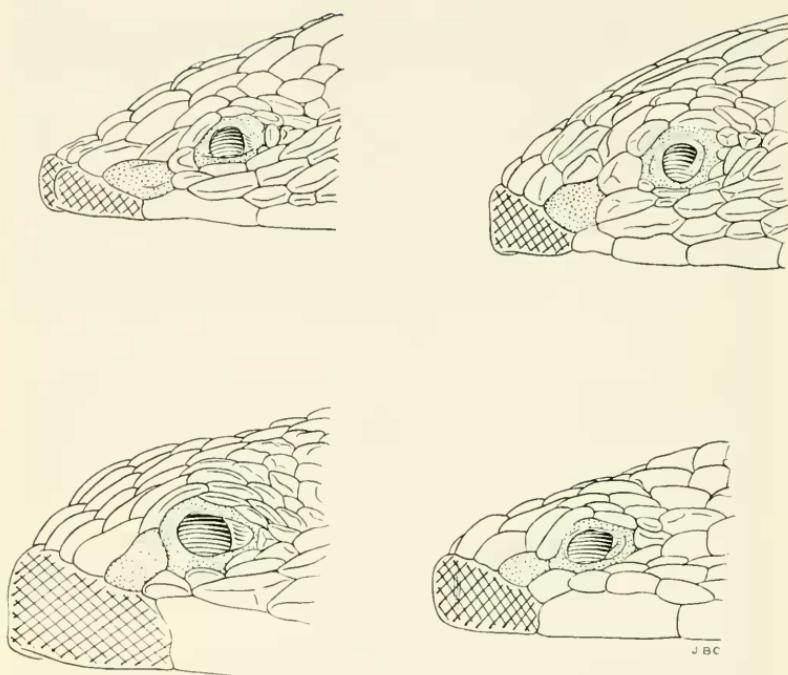


Figure 3. Nasal rostral relationships. Upper left: *Anolis biporcatus biporcatus*, MCZ 15426. Upper right: *A. b. parvaauritus*, MCZ 78942. Lower left: *A. apollinaris*, Munich 422. Lower right: *A. fraseri*, MCZ 43772.

its simplicity but upon its association with other characters regarded as primitive and on its occurrence in species regarded on other grounds as primitive.) The variation in *apollinaris* is in the direction of the pattern in *biporcatus*, but there is no overlap. This is a sharp and clear distinction.

2. *Supraciliary scales* (Fig. 4). Again the pattern of this area tends to be species specific and again the condition in *apollinaris* tends to be simpler and perhaps more primitive than that of *biporcatus*. The common pattern in *biporcatus* is indeed unusual (though not unique). Two patterns are common for the supraciliary region of anoles: (1) one or more elongate supraciliaries followed by undifferentiated granules; (2) one or more elongate supraciliaries followed by a double series of enlarged scales rather even in size.

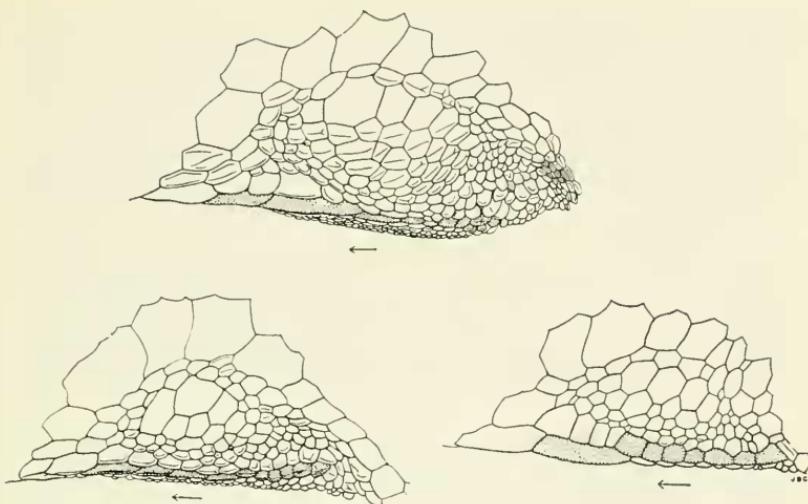


Figure 4. Supraciliary area. Top: *Anolis apollinaris*, Munich 422. Lower left: *A. b. biporcatus*, MCZ 15426. Lower right: *A. fraseri*, MCZ 43772.

A. biporcatus, exhibiting several rather short supraciliaries grading into large scales that tend to grade again into granules, presents a condition hardly more frequent than that of *A. fraseri* with its series of quadrate scales along the whole supraciliary margin, the first of these sometimes elongate.

3. *Scales around interparietal.* In general, the degree of enlargement of scales around the interparietal is a good specific character in *Anolis*. Particularly valuable may be the degree of enlargement of the scales posterior to the interparietal as compared with the adjacent dorsal or supratemporal scales. There may be rapid intergradation of enlarged scales lateral to the interparietal into much smaller dorsal and supratemporal scales, or the scales behind the interparietal may be sharply and conspicuously larger than dorsal or supratemporal scales (as in some *apollinaris*). The two subspecies of *A. biporcatus* differ in this regard. *A. apollinaris* is variable; perhaps the variation is geographic, but there is not enough material to say.

4. *Ear shape and position.* The ear of *apollinaris* is quite different from that of either southern or northern *biporcatus*. It is

closer in size to that of southern *biporcatus* but quite distinct in its obliquity, a rather unusual feature.

5. *Ventral keeling.* This character is minor. Keeled ventrals may be a good species character, but there are many instances of intraspecific variability, both geographic and (typically qualitatively less extreme) at a single locality. *A. apollinaris* has the ventrals more weakly keeled than either subspecies of *biporcatus*.

6. *Toe lamellae.* The number of toe lamellae is an extremely useful character in *Anolis* and very characteristic of species. It is, however, subject to variability (a range of 6 or 7 is quite usual) and overlap is, as in the present case, frequent. *A. apollinaris* tends to a higher number of toe lamellae than either subspecies of *biporcatus*.

7. *Color.* I have no descriptions of color in life of *apollinaris* and the varying colors of *biporcatus* as preserved (it is uniform green in life) do not make comparison very easy. Boulenger described the type female as "Dark olive above and on the sides, with a fine blackish network, head and a vertebral band pale, the latter with narrow transverse processes; small round light spots on the sides and tail; forearm, tibia and lower parts pale green."

The Brussels specimen has preserved its pattern rather well. Description follows: Head greyish. A dark streak from back of eye to shoulder, there merging with dark flanks. Below this, labials and nape lighter, their color continuous with the smudged grey of the throat. A light brown middorsal zone, irregularly darker laterally, bordered on each side by a narrow grey line. Flanks dark brown with indications of white spots or broken narrow vertical white bars. Forelimbs obscurely annulate, hind limbs boldly so. Tail above with longitudinally oval light spots with irregularly dark centers. Belly lighter than any part of dorsum but still heavily infuscated. Tail below lighter still.

The new specimens resemble the Brussels specimen in head coloration, as the British Museum type now does; presumably the latter differs from Boulenger's description as a result of change during preservation.

A. apollinaris, when compared with *A. biporcatus*, differs in few and superficially trivial ways. The ventrals are less strongly keeled. There are fewer scales between nostril and rostral: one or more rather than two or three. The color is quite unlike anything I have seen in *biporcatus*. I am neither confident that this form is a full

species nor convinced that it is not. It is certainly not to be confused with Mexican or Central American *biporcatus*, nor with the south Colombian-Ecuadorian population, nor does it resemble the two Venezuelan specimens of that species. Whether it is distinct from, or intergrades with, some of the other Colombian or the Ecuadorian populations is a matter for future discovery. Provisionally, since it was described as a species, it may remain so allocated.

A. biporcatus has the distribution of a recent immigrant into South America, extending from Panama through the Choco region of Colombia down into Ecuador west of the Andes and extending eastward through the Santa Marta Mountains into western Venezuela. *A. apollinaris*, now recorded from Antioquia, Caldas, and Cundinamarca, may be supposed to have arisen from *A. biporcatus* by isolation and subsequent minor modification in the central Andean regions of Colombia. Since it has some primitive features (e.g., nasal-rostral relationship) and since it has reached species status, it may represent an earlier invasion of South America than that which resulted in *A. b. parvauritus* Williams and the Venezuelan specimens of *A. b. biporcatus*.

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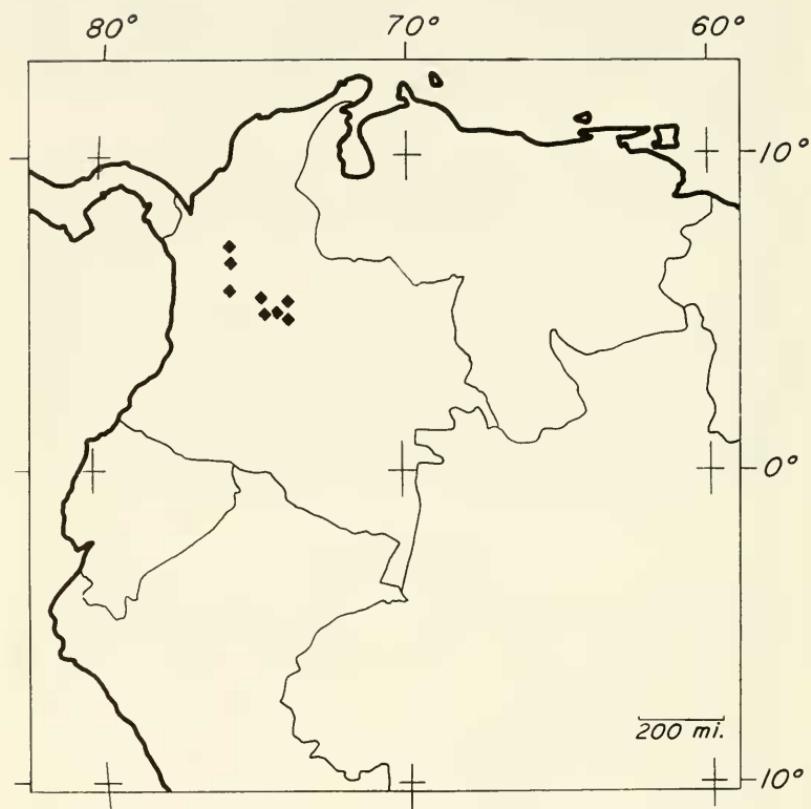


Figure 5. Map of the distribution of *Anolis apollinaris* in central Colombia.

TABLE 1

	<i>apollinaris</i>	<i>b. biporcatus</i>	<i>b. parvauritus</i>
scales across snout	9-13	7-11	8-13
scales between nasal and rostral	0-1	2-3	2-3
scales between supraorbital semicircles	2-4	1-4	0-3
supraciliaries	1-2 elongate plus series of small scales of rather uniform size	usually 3-4 short supraciliaries plus a series of small scales of variable size	as in <i>biporcatus</i>
scales behind interparietal	variable, slightly to abruptly larger than dorsals	abruptly larger than dorsals	grading gradually into dorsals
scales separating interparietal from semicircles	3-5	3-6	3-7
loreal rows	5-8	5-10	6-9
supralabials to center of eye	7-8	8-11	7-12
ear	small to moderate	moderate to large, vertical	small
ventrals	weakly keeled	strongly keeled, mucronate	strongly keeled, mucronate
lamellae under phalanges ii and iii of fourth toe	25-27	22-26	22-26